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MORPHOLOGICAL DEVELOPMENT AND DISTRIBUTION OF PARALARVAE AND JUVENILES OF PURPLEBACK FLYING SQUID *STHENOTEUTHIS OUALANIENSIS* (OMMASTREPHIDAE), IN THE SOUTHEASTERN ARABIAN SEA

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ARABIAN SEA
PARALARVAE
JUVENILES
STHENOTEUTHIS OUALANIENSIS

ABSTRACT. – The occurrence, distribution and morphological development of paralarvae and juveniles of *Sthenoteuthis oualaniensis* from the Arabian Sea (8°-17°N and 64°-76°E) are presented and discussed based on 32 exploratory surveys conducted during 2010-2013. The results indicated that the spawning grounds of *S. oualaniensis* may be in the southeastern Arabian Sea around the Lakshadweep Archipelago (09°04'N-15°04'N, 73°44'E-75°36'E). Detailed morphological studies of the planktonic paralarvae (rhynchoteuthions), revealed the presence of three stages based on the shape and relative size of the proboscis: stage 1 (1.47-1.78 mm DML), stage 2 (2.07-5.17 mm DML) and stage 3 (5.17-9.18 mm DML). The observations revealed that the switch from paralarvae to juvenile occurs between 8.7 and 10 mm DML. Aging studies using statoliths revealed that the paralarval period ends 36 to 52 days after hatching, with the growth rate ranging from 0.14 to 0.21 mm DML. The results also indicate that the species spawns near the continental shelf edge, and that paralarvae migrate to oceanic waters thereafter.

INTRODUCTION

Ommastrephid squids are economically important on a global scale as they make a significant contribution (58 %) to the total cephalopod production (4.07 millions tons, 2013) from the world oceans (FAO, 2016). These squids are important functional elements of tropical oceanic ecosystems and are potential fishery resources (Zuyev *et al*. 2002). The purpleback flying squid *Sthenoteuthis oualaniensis* (Lesson, 1830) is one of the most abundant and largest oceanic squids in the tropical and subtropical waters of the Indo-Pacific region and the Arabian Sea (Yamanaka *et al*. 1976, Silas *et al*. 1985, Young & Hirota 1998). They have a complicated population structure and morphological distinctions exist between different forms (Clarke 1965, Nesis 1993). Morphological features, geographical distribution and trophic relationships of *S. oualaniensis* change fundamentally during ontogeny (Zuyev *et al*. 2002). It is also known as the "Master of the Arabian Sea" due to its high abundance, large size, short life-span, fast growth and near monopoly of the higher trophic niche of the ecosystem (Chesalin *et al*. 1995). Though the Arabian Sea is considered one of the richest regions for this species in the Indian Ocean (Zuyev *et al*. 2002), the resource is not the object of a directed fishery by any of the bordering nations. A small-scale commercial jigging fishery for these squids is operated by Chinese distant water fishing fleet (Chen *et al*. 2008), and India has embarked on an ambitious project to explore these resources from the southeastern Arabian Sea (Mohamed *et al*. 2014). Partly because of the absence of a directed fishery, many aspects of the reproductive biology, distribution and ecology of squid in this area are poorly described.

Previous studies on this species have focused on taxonomy from the Pacific Ocean (Okutani & Tung 1978, Harman & Young 1985), and distribution patterns of *S. oualaniensis* paralarvae from Hawaiian waters (Bower *et al*. 1999a). Aspects of the life history, especially the reproductive biology and longevity of this species, are poorly understood. The spawning time and location of its spawning grounds are as yet unknown in the Arabian Sea. Knowledge of the early life stages of cephalopod distribution and abundance patterns are useful to determine spawning area, season, and its periodicity (Bower *et al*. 1999b).

Preliminary reports on the occurrence of paralarvae (also called rhyncoteuthions) and juveniles of *S. oualaniensis* from the Arabian Sea include those by Chun (1903), Silas (1968) and Aravindakshan & Sakthivel (1973). As part of the faunal composition study of cephalopods, preliminary information on paralarvae and juveniles from the Arabian Sea was presented by Chesalin & Zuyev (2002). However, information on paralarval and juvenile abundance, its growth and morphometric aspects from Arabian Sea are lacking. The present study provides information on the distribution, morphological development, and relative growth of paralarvae and juveniles of *S. oualaniensis* in the southeastern Arabian Sea, which could lead to the identification of spawning

grounds of the species. We also assess growth based on statolith analysis.

MATERIALS AND METHODS

Study area: The study covered the western Indian Ocean from 8° to 17°N and 64° to 76°E, which includes the eastern and central Arabian Sea over bottom depths ranging from 100 to 4000 m. Exploratory surveys were undertaken from September 2010 to March 2013 by the *MV Titanic,* a commercial trawler converted for squid jigging. Oceanographic and biological sampling was conducted at 58 stations (Fig. 1). Due to rough weather conditions during the monsoons, research cruises were not undertaken from May to August.

Sampling: Cruises were typically coinciding with the new-moon phase in every month. Stations were occupied from dusk to morning (17.00 to 04.00 h) during which time metal halide lights (1500×18 nos) were used to illuminate the area around the vessel. At each station, zooplankton sampling included surface hauls (10 minute duration) at 2 knots using a circular zooplankton net (50 cm diameter) with a mesh size of 200 µm (KC Denmark, Model 23.100-WP-2) equipped with a calibrated flowmeter. Small paralarvae were collected as part of the zooplankton samples. Larger paralarvae and juveniles were opportunistically caught using a scoop net with 2 mm mesh size. A total of 128 juveniles were collected, from which 54 were used for morphometric analysis. Bottom depth and position of each tow were determined using SANSUI GPS. The oceanographic parameters

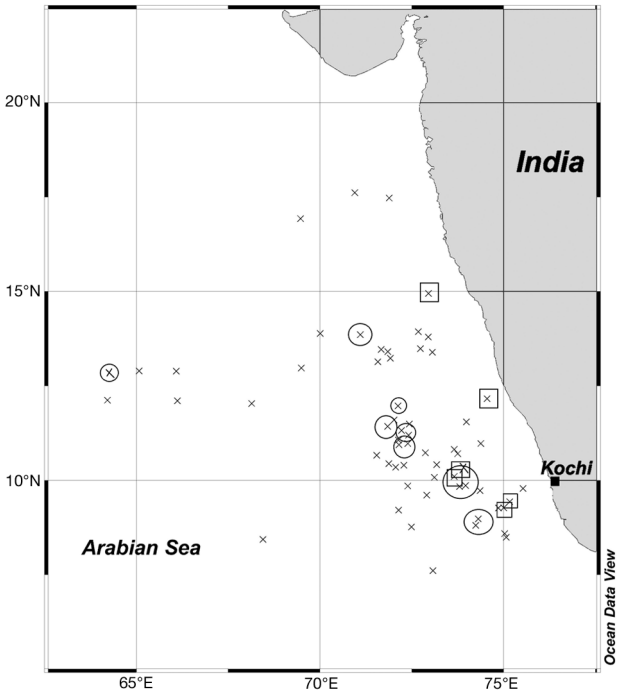

Fig. 1. – Map showing the study area, sampling stations (×) and location of paralarvae (⊗) and juvenile (☒) *S. oualaniensis* observed during October 2010 to March 2013 in the Arabian Sea.

(salinity, pH, temperature and dissolved oxygen) were measured by using a multiparameter probe (YSI, Model 650 MDS).

Abundance estimation: The relative abundance of paralarvae at all stations was calculated as the number of individuals (N) per 1000 m^3 of water volume filtered. The volume of filtered water in m^3 was estimated using the flowmeter reading in the sampler (L [flowmeter reading] × 0.3 [impeller pitch factor]) and the area of the plankton net opening (r) as $V = (L \times \pi \times r^2 \times 1000)$. The abundance of paralarvae were estimated by using formula, Abundance (number/1000 m^3) = (N/V) × 1000, where, N = number of paralarvae and V = volume of filtered sea water. Juvenile biomass was estimated at all stations based on Zuev *et al*. (1985) using the formula, B = (N × W) / (V × D), where, N = number of squids observed during 1 h of observation, W = average weight of different size groups, V = drift speed of the ship (3.7 km/h) and D = width of the light zone (9 m). The estimated biomass value in each station was converted into numbers by dividing the value with average weight. A limitation of this light-trap method is that it can sometimes result in over-estimation. The average weight of different size group was estimated by weighing a subsample of specimens in the laboratory.

Identification and morphometric measurements: All larval squid samples from individual tows were preserved in 5 % buffered formalin on-board. In the laboratory, they were identified, sorted, counted, and measured. Identification of paralarvae was done based on key morphological characters described by Okutani & Tung (1978) and Sweeny *et al*. (1992) with the help of a binocular microscopic and image analyzing system (Leica DFC 295). Eleven length measurements of external morphology such as dorsal mantle length (DML) mantle width (MW), head length (HL), head width (HW), arm length I, II, III and IV (AL I, AL II, AL III, AL IV), fin length (FL), fin width (FW) and tentacle length (TL) were recorded according to Roper & Voss (1983) for paralarvae and juveniles. The measurements were taken with an ocular micrometer for small paralarvae, and a digital vernier caliper for larger paralarvae and juveniles. Key indices were calculated for body dimensions relative to mantle length as (body dimension/mantle length) × 100.

The morphological developments in paralarvae were divided into three stages based on the relative length of the proboscis and its separation into two tentacles (Roper & Lu 1978). Briefly, in stage 1 the proboscis was short to moderate and in stage 2 the proboscis length almost doubles. Stage 3 was morphologically defined as the beginning of the proboscis separation to the end of the separation into two tentacles (Table I). Complete splitting of the proboscis was considered the end of the paralarval stage (Young & Harman 1988). Morphologically, juveniles were similar to adults.

Statistical analysis: Regression analysis was used to compare the log-transformed body dimensions and the DML of paralarvae and juveniles. The following equation was used $y = aDML^b$, where y is the length of the dimension of interest, *b* is the slope and '*a*' is the initial index (Zeidberg 2004). When

Table I. – Ontogenetic changes during morphological development of paralarvae of *S. oualaniensis* from southeastern Arabian Sea.

Paralarval Stage	Sample Numbers	Size range (mm)	Number of arms	Size of proboscis (mm)	Tentacular Index	Proboscis characters	Mean depth of stations (m)
Stage 1	5	1.47-1.78	3 pairs	0.7-0.81	38.2-48.3	Short proboscis	678
Stage 2	27	2.07-5.17	4 pairs	1.28-2.36	51.7-81.4	Long proboscis	1757
Stage 3	94	5.17-9.18	4 pairs	0.95-2.31	6.84-34.1	Proboscis division	1889

$b > 1$, the given body dimension was growing faster than the DML (positive allometric growth), when $b = 1$, the two dimensions had isometric growth, and for $b < 1$ the DML was growing slower than the given body dimension (negative allometric growth). Analysis of covariance (ANCOVA) was used to test for significant differences in morphometric relationship between paralarvae and juveniles.

Statolith aging: The statoliths of 22 alcohol preserved paralarvae (stage 3) and early juveniles were extracted and, prior to fixing, the total length of the statolith (TSL) was recorded. One statolith from each pair was used for aging. Each statolith was first attached to a microscopic slide with the anterior (concave) side facing up with crystal bond mounting medium. After drying (usually 5 minutes), the paralarval and early juvenile statolith growth rings were counted using a Nikon (*Eclipse-80i*) microscope. Juvenile (15-45 mm DML) statoliths were also mounted in a similar way and polished with fine sandpaper (Grit #1500). The date of hatching was estimated by back calculation from the time of capture, assuming that the increments formed daily. The daily growth rate, DGR ($mm.d^{-1}$) was calculated as $DGR = (W_2 - W_1) / T$ following Arkhipkin & Perez (1998), where W_1 and W_2 are dorsal mantle length (DML) at the beginning and end and T is total age in days.

RESULTS

Environmental parameters

Average sea surface temperature (SST) was about 28 °C throughout the study, salinity ranged from 32.88 to 34.58 psu and chlorophyll-*a* from 0.1 to 3 $mg.m^{-3}$ over the entire study area.

Paralarval and juvenile distribution

Paralarvae were observed at 6 of the 58 stations surveyed from October 2010 to March 2013. High abundance of paralarvae was observed 46 nm west of Kollam (09°03'N; 75°36'E) in February 2011 and high abundance of juveniles was observed 60 nm southeast of Kalpeni Island (09°44'; 74°37') in January 2012.

Morphological characters

Paralarvae of *S. oualaniensis* are characterized by equal-sized suckers on the proboscis. There were three chromatophores on the anterior dorsal mantle and one on the posterior dorsal mantle. Paralarvae larger than 4 mm DML had a photophore on the ventral side of each eye and possessed a mantle funnel locking apparatus with an inverted T shape. Three different growth stages (stage 1 to 3) could be differentiated based on the size and shape of the proboscis and the relative sizes of suckers on its proboscis tip (Table I).

Paralarval stage 1

The paralarval stage 1, measuring 1.47 to 1.78 mm DML, was characterized by eight suckers on the proboscis, among which the two lateral suckers were slightly enlarged. The length of the proboscis (0.71 mm to 0.81 mm) in relation to DML (tentacular index) was short to moderate (mean = 44.4; range = 35.8-48.3). The fourth arms were not differentiated at this stage. The arm formula was II > III > I. The chromatophore pattern in the mantle could not be observed in some specimens due to loss of colouration from formalin preservation. Five specimens of stage 1 were obtained from shallow waters, three at 09°03'N 75°36'E (684 m depth) and two at 15°04'N 73°00'E (264 m depth) in February and April 2011, respectively (Fig. 2). Among them, two specimens were damaged during plankton net towing.

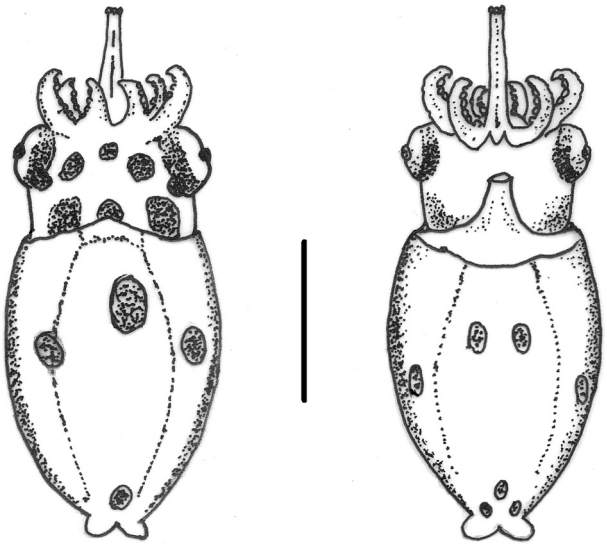

Fig. 2. – Stage 1 paralarvae of *S. oualaniensis* (dorsal and ventral view). Scale bar = 1 mm.

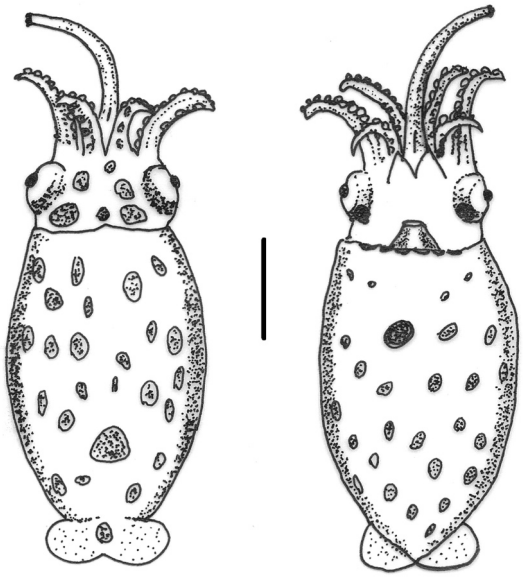

Fig. 3. – Stage 2 paralarvae of *S. oualaniensis* (dorsal and ventral view). Scale bar = 1 mm.

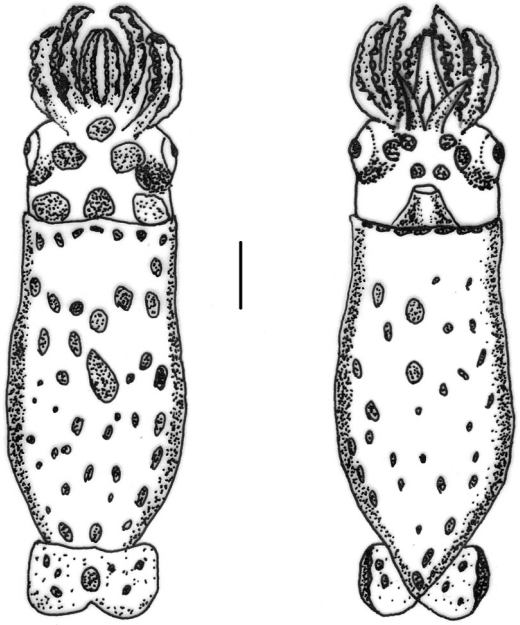

Fig. 4. – Stage 3 paralarvae of *S. oualaniensis* (dorsal and ventral view). Scale bar = 1 mm.

Paralarval stage 2

Rhynchoteuthions ranged in size from 2.07 to 5.17 mm DML and were characterized by all the suckers on the tip of the proboscis being of similar size. The proboscis was very thin and narrow, and it was moderately long to very long (mean tentacular index = 72.4; range = 51.7-81.5). Arms I, II and III were well developed (Fig. 3). Stage 2 paralarvae were observed at four stations. Twenty-seven stage 2 specimens were observed from 09°03'N to 11°41'N and 73°00'E to 75°36'E having a bottom depth ranging from 931 to 2161 m.

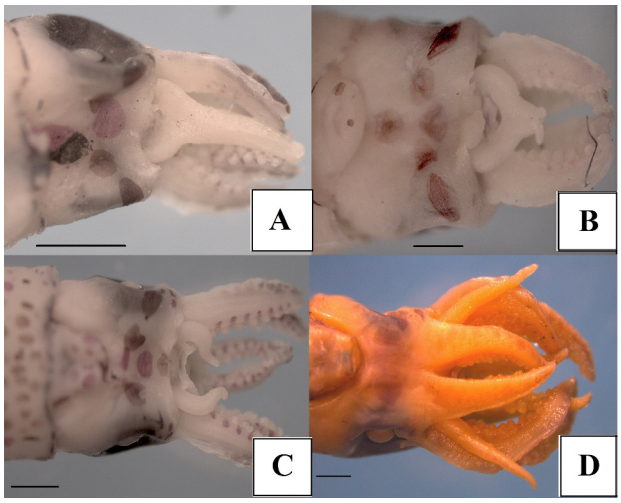

Fig. 5. – **A**: Stage 3 paralarva showing beginning of proboscis separation at the base; **B**: Stage 3 in final paralarval period; **C**: Fully separated proboscis at the beginning of juvenile stage and **D**: Juvenile with functional tentacle. Scale bars = 1 mm. The specimen fourth arm was manually removed for getting a better view.

Paralarval stage 3

Stage 3 paralarvae were characterized by a relatively short, robust proboscis and all the suckers on the tip of the proboscis were of similar size (Fig. 4). A triangular opening was observed at the base of the proboscis with a shallow longitudinal groove, the "splitting groove", which runs along the proboscis. As the squid grows, this triangular hole widens between the bases of the proboscis and finally separate as two functional tentacles (Fig. 5A, B). In stage 3 proboscis separation was initiated and completed and this is considered as the end of larval stage (Fig. 5C, D). The dorsal and ventral sides of the head region have six large chromatophores, and the mantle has a number of small chromatophores. Arm IV was relatively small. The stage 3 specimens ranged from 5.17 to 9.18 mm DML with a tentacular index ranging from 6.8 to 34.1 and mean index of 22.6. Our observations indicated that the transition from paralarva to juvenile occurs between 8.70 and 10 mm DML. Therefore, all specimens less than 8 mm DML were classified as rhynchoteuthions and all individuals greater than 10 mm DML as juveniles. Stage 3 individuals were observed at 10°14'N; 73°44'E in October 2010 and 09°44'N; 74°37'E in January 2011 in bottom depths ranging from 1830 to 2300 m.

Comparison of body dimensions

Of the 126 paralarvae collected, 5 were stage 1 paralarvae (1.47 to 1.78 mm DML), 27 were stage 2 (2.07 to 5.17 mm DML) and 94 were stage 3 (5.17 to 9.18 mm DML). Relative to dorsal mantle length, mantle width showed strong negative allometry throughout the paralarval stage ($b = 0.14$). In young paralarvae, the mantle width

index was 71.3 on average, and at the end of paralarval stage it was 33.1 (Fig. 6A). The head length index ranged from 20.6 to 40.3 and decreased with increasing mantle length (b = 0.16) (Fig. 6B). Head width showed nega-

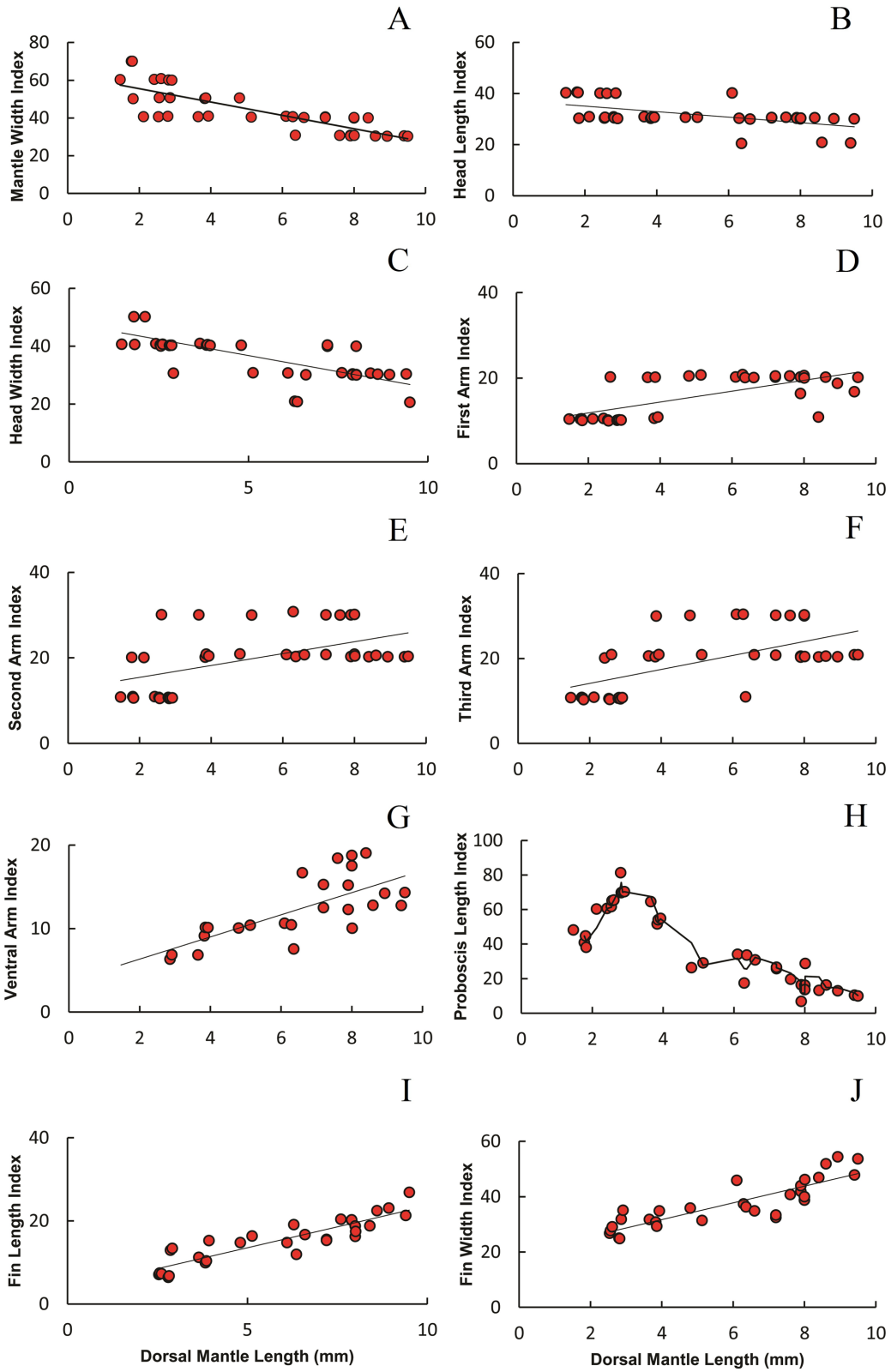

Fig. 6. – Relationship between body dimensions and dorsal mantle length (DML) of *S. oualaniensis* paralarvae. **A**: Mantle width index, **B**: Head length index, **C**: Head width index, **D**: First arm index, **E**: Second arm index, **F**: Third arm index, **G**: Ventral arm index, **H**: Proboscis length index, **I**: Fin length index and **J**: Fin width index.

tive allometry throughout the paralarval stage (b = 0.15). Head width was slightly narrower than the mantle width throughout paralarval development and the index ranged from 20.8 to 50.2 (Fig. 6C). In the paralarval stage 1, the head was half withdrawn into the mantle cavity in preserved specimens. Head withdrawal was not observed in stages 2 and 3. Separation of the proboscis began at stage 3 and its index ranged from 6.8 to 34.1 (Fig. 6H). The arm formula was II > III > I in individual less than 3.65 mm DML. From 3.65-9.5 mm DML, the arm formula was II > III > I > IV (Fig. 6D-F). In stage 1 the ventral arm was absent, at average DML 2.8 mm, the fourth arm appeared as a tiny point near the base of proboscis. After that the ventral arm grew fast, from 0.63 mm at 2.8 mm DML to 1.90 mm at 8.9 mm DML (Fig. 6G).

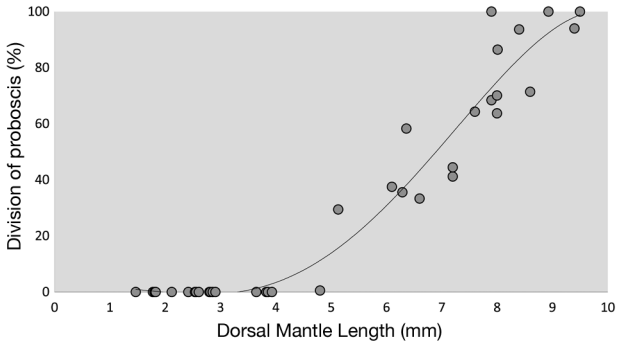

Fig. 7. – Progress of proboscis divisions with increasing DML in *S. oualaniensis* paralarvae.

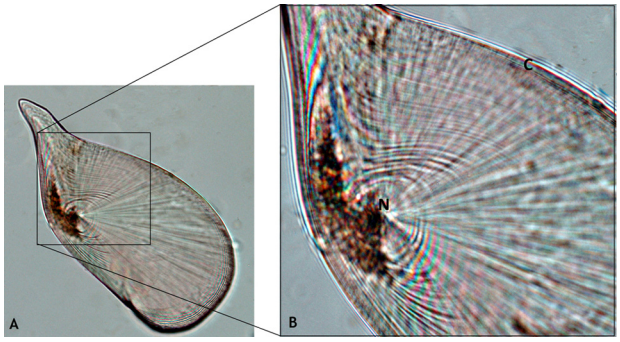

Fig. 8. – Light micrograph of statolith of Paralarvae (DML-8.3 mm). **A**: Whole statolith; **B**: Growth increments of paralarval statolith. Nucleus (N) and Check mark (C).

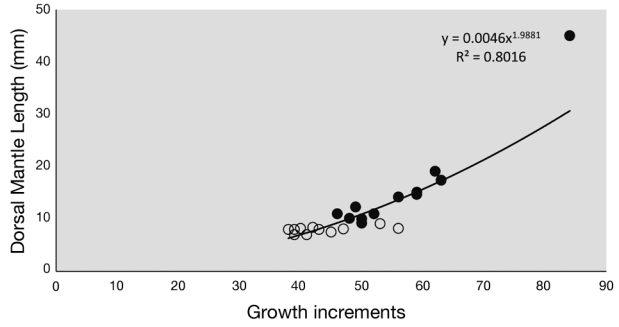

Fig. 9. – Relationship between dorsal mantle length against number of growth increment in *S. oualaniensis* paralarvae (open circle) and juveniles (closed circle).

In the initial stages, the fins were rudimentary and terminal. They were small and oval in shape and became larger with age. Fin length and width indices ranged from 7.0 to 26.8 and 24.8 to 53.6, respectively (Fig. 6I, J). In stage 3, the fins and arms are well developed; they can be moved freely. Proboscis division started in sizes greater than 5 mm DML and was completed between 7.8 to 9.5 mm DML (Fig. 7). In early juveniles, the tentacles were weakly developed and were about 50 % the length of arm III.

Paralarval growth

The statoliths were pear shaped and ranged in size from 200 to 240 µm (Fig. 8). The relationship between DML and total statolith length was linear in all samples (r^2 = 0.71), and the number of growth rings ranged from 36 to 52 (5.5 to 9.0 mm DML). The daily growth rate ranged from 0.14 to 0.21 mm DML/day with an average of 0.18 mm DML/day (Fig. 9).

Juveniles

Juveniles were observed near the surface at night and they were attracted by the lights. They were identified based on the presence of a very pronounced intestinal photophore and mantle funnel fusion. The juvenile schools ranged from 20 to 50 individuals of the same size. Medium sized juveniles (40 to 50 mm DML) were observed to leap out of water and glide up to distance of approximately 20 m.

Morphological characters

A total of 54 juvenile individuals (9.15 to 67.6 mm DML) were sampled. Comparisons of length dimensions show the relative growth of juveniles (Fig. 10). In comparison to dorsal mantle length, mantle width shows negative allometry (b = 0.14) indicating that the squid grew more in length than in width. The mantle width index ranged from 16.6 to 33.7 (Fig. 10A). Juveniles had a longitudinally elongated, slender cone shaped mantle. Head length index ranged from 16.4 to 30.6, decreasing with increasing DML (b = 0.30) (Fig. 10B). Head width also showed negative allometry (b = 0.27), and head width index ranged from 14.0 to 26.6 (Fig. 10C).

The stage 3 paralarval arm formula (II > III > I > IV) remained in the early juvenile stage up to a DML of 26 mm before changing to IV > III > I > II. In the initial stages, the tentacles were smaller than the arms, and the tentacular club was not developed (Fig. 10D-G). After 12 mm DML, the tentacles and tentacular club development was faster (Fig. 10H). In juveniles of 17 mm DML, the arms were longer, and the dactylus was already formed. When they reached 30 mm DML, the growth rate of the arms decreased. Simultaneously, there is rapid

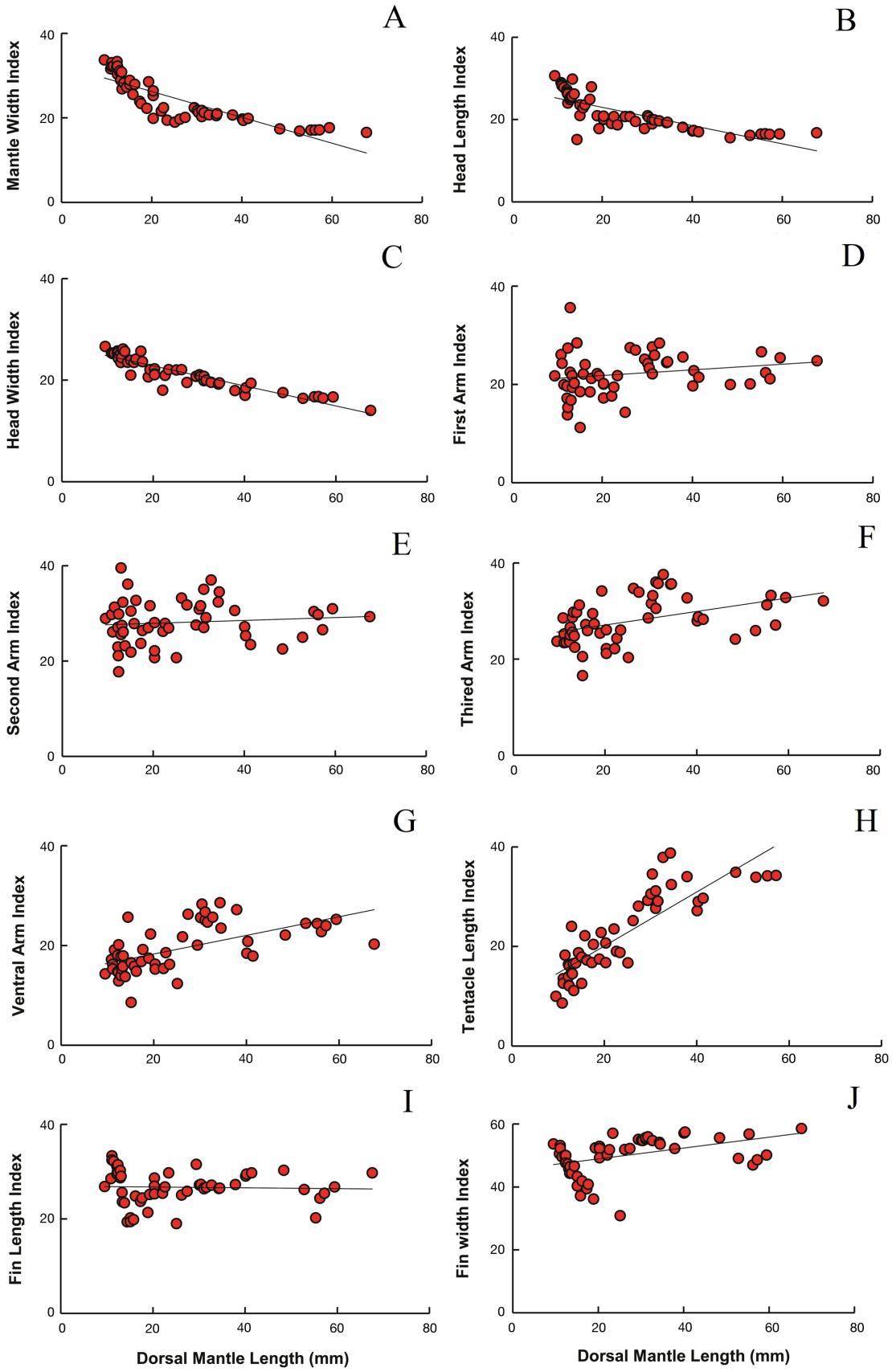

Fig. 10. – Relationship between body dimension and dorsal mantle length (DML) of *S. oualaniensis* juveniles. **A**: Mantle width index; **B**: Head length index; **C**: Head width index; **D**: First arm index; **E**: Second arm index; **F**: Third arm index; **G**: Ventral arm index; **H**: Tentacular length index; **I**: Fin length index and **J**: Fin width index.

elongation of the tentacles with a well-developed club. In the juvenile stage, the surface area of the fins grows positively and has a triangular shape. The indices of fin length and width ranged from 19.4 to 33.3 and 30.9 to 58.5, respectively (Fig. 10I, J). Head withdrawal was not observed in preserved juveniles.

The slopes obtained for body dimension relationships between paralarvae and juveniles showed no significant difference between DML-MW (ANCOVA, $P = 0.12$) and DML-HW ($P = 0.96$), whereas, the relationship between dorsal mantle length and HL, Arm I, II, III, IV, TL, FL and FW were significantly different (Table II).

Age and growth

Early juveniles had 46 growth rings and growth rates ranged from 0.18 to 0.84 mm DML/day. Some juvenile statoliths had a check mark between 40 and 60 increments (Fig. 8). A juvenile of DML of 45 mm had a growth rate of 0.84 mm DML/day (Fig. 9).

Geographical distribution of paralarvae and juveniles

Stage 1 paralarvae were observed on the continental shelf slope where the bottom depth ranged from 425 to 931 m, which is presumed to be very close to the site where they hatched. Stage 2 paralarvae were observed in the outer region of the shelf edge and near to the Archipelago Islands (Lakshadweep Islands) where the bottom depth ranged from 931 to 2140 m. They co-occur with stage 1 and stage 3 individuals. Stages 1 and 2 paralarvae were found together at 09°03'N-75°36'E, and stages 2 and 3 were found together at 10°14'N-73°44'E, and 09°44'N-74°37'E. The highest abundance of paralarvae was observed in the eastern side of Lakshadweep archipelago at salinities of 34-35 psu, temperature higher than 28.48 °C and at bottom depths less than 1500 m. Fewer individuals were observed in the oceanic region where the depth ranged from 1638 to 2140 m (Table III; Fig. 11).

Juveniles were widely distributed from the continental shelf edge to deeper oceanic regions. A high abundance was observed at 9°44'N-74°37'E (2400 m) but lower abundances were observed at 12°07'N-72°02'E (1440 m). They were observed at salinities of 34-35 psu and at bottom depths > 1400 m. The numbers of juveniles were low where bottom depths were < 1500 m (Fig. 11). A high abundance of juveniles was observed in January during both years and comparatively less abundance was observed in October and November (Table IV).

Table II. – Summary of comparisons of regression equations based on analysis of covariance. **: P < 0.01, ***: P < 0.001, ns = not significant.

Variables	Mean square	F-Ratio	P-value	Significance
MW	0.02	2.4082	0.1243	ns
HL	0.17	13.9344	0.0003	***
HW	0.00	0.0021	0.9633	ns
A1	0.45	9.2279	0.0031	**
A2	0.19	4.5710	0.0353	**
A3	0.24	7.2856	0.0084	**
A4	1.75	21.7951	0.0000	***
TL	17.76	62.1453	0.0000	***
FL	0.44	71.0562	0.0000	***
FW	0.44	21.7582	0.0000	***

Table III. – Estimated abundance of paralarvae of *S. oualanienis* from southeastern Arabian Sea.

Months	Latitude (N)	Longitude (E)	Depth (m)	No./1000 m³	Stage	Size range (mm)
October 2010	10°14'N	73°44'E	2140	191	Stages 2 & 3	4.95-8.64
January 2011	09°44'N	74°37'E	1638	217	Stages 2 & 3	2.98-9.16
February 2011	09°03'N	75°36'E	931	270	Stages 1 & 2	1.55-3.07
April 2011	15°04'N	73°00'E	425	38	Stage 1	1.47-1.87
February 2012	10°29'N	73°56'E	2161	174	Stage 2	2.30-3.38
March 2012	11°41'N	74°17'E	1918	80	Stage 2	2.07-3.45

DISCUSSION

Sthenoteuthis oualaniensis is the only ommastrephid known from the Arabian Sea (Silas 1968, Piatkowski *et al*. 1991, Sweeny *et al*. 1992). Paralarvae have a distinctly different mode of life from the adults, with an end point identified by ecologically significant changes in morphological characters (Young & Harman 1988). These rhynchoteuthions are characterized by the absence of the fourth (ventral) pair of arms and the fusion of the tentacles into a single appendage. Separation of the fused tentacles is considered the end of the paralarval stage. Ommastrephid squids or "flying squids" are characterized by the smallest paralarvae among the cephalopods (O'Dor & Lipinski 1998). In *S. oualaniensis*, the paralarval stage terminates with the separation of the tentacles between 9 and 10 mm DML while the juvenile period ends around 100 mm DML, with the development of mantle photophores (Young & Harman 1988). Paralarval growth of *S. oualaniensis* was characterized by rapid growth of arms and fins while the mantle width, head length and head width have comparatively slower growth. Another significant morphological change during the paralarval stage was the lengthening, shortening and splitting of the proboscis. In teuthoid squids, fast growth and slendering of the body as a result of relatively slow growth of mantle

Table IV. – Approximate monthly abundance of juveniles *S. oualanienis* in southeastern Arabian Sea based on light trap data.

Months	Number/ km²	Latitude (N)	Longitude (E)	Depth (m)
Oct-10	130,030	10°14’	73°14’	2160
Nov-10	36,036	14°00’	72°59’	1500
Jan-11	39,039	13°00’	65°59’	4400
Jan-11	10,511	09°30’	74°56’	2460
Feb-11	12,613	10°29’	73°58’	2100
Jan-12	3,003,003	09°44’	74°37’	2400
Jan-12	57,357	11°00’	72°00’	1530
Jan-12	37,538	11°19’	72°00’	1600
Jan-12	28,529	10°23’	73°20’	1900
Feb-12	2,102	12°07’	72°02’	1680
Feb-12	1,201	11°15’	71°58’	1440
Feb-12	37,538	11°00’	72°00’	1500
Feb-12	6,006	10°32’	72°57’	2000
Mar-12	12,012	11°41’	74°17’	1551

width is probably selected to boost the efficiency of jet propulsion, which is ultimately useful for efficient predation (O’Dor 1982).

In stage 2 rhynchoteuthions are able to withdraw their head into the mantle cavity was observed in some preserved paralarvae. The head withdrawal behavior has also been reported in paralarvae of other ommastrephids: *Illex illecebrosus* (O’Dor *et al*. 1985), *Illex argentines* (Vidal & Haimovici 1998), and *Todarodes pacificus* (Shigeno *et al*. 2001). The head withdrawal might be associated with suspension feeding (O’Dor *et al*. 1985, Vidal & Haimovici 1998). This behavior is provoked by mechanical (Hamabe 1962) or chemical (Okiyama 1965) stimuli and may also be a defensive reflex (Shigeno *et al*. 2001).

At hatching, ommastrephid paralarvae have a very short proboscis and a large internal yolk sac (O’Dor *et al*. 1985, Sakurai *et al*. 1995). Because of the food reserve in the internal yolk sac of stage 1 *S. oualaniensis*, they do not need to capture food. By four days post hatch, (stage 2) the yolk is absorbed and the yolk sac is nearly gone necessitating elongation of the proboscis (Sakurai *et al*. 1995). The paralarvae need to feed but cannot move freely, and they drift with the water current and at this stage, the long proboscis may act like an elephant trunk to capture prey (Sakurai *et al*. 1995). After complete division of the proboscis, the newly formed tentacles are fragile and thinner than the arms without the development of tentacular clubs. The early juvenile stages of *S. oualaniensis* also display paralarval behavioral characteristics and prefer the same oceanographic and feeding conditions as evident from the co-occurrence of stage 3 along with early juveniles from the same location. Recent studies show that ommastrephid paralarvae are primarily detritus feeders and ontogenetic shift of diet from detritivore suspension feeding to active predation represents a unique life strategy among cephalopods allowing ommastrephid squids to take advantage of an almost ubiquitous and accessible food resource during their early stages (Fernández-Álvarez *et al*. 2018).

Stage 1 paralarvae of *S. oualaniensis* feed using the fused proboscis (Shea 2005). We observed fast arm growth in stage 2 and in initial portions of stage 3, but in the final paralarval period, the growth index decreased probably because the arms reached the size sufficient for grasping prey. After separation of proboscis the newly formed tentacles are fragile and thinner than the arms and are probably not suitable to capture preys (Vidal 1994). After 17 mm DML, the tentacles are longer than the arms and form tentacular clubs that allow the capture of a broader variety of preys. This event represents a major change in the life history of this species (Young & Harman 1988). Stage 3 paralarvae and early juveniles were found together in same station suggesting that they prefer similar oceanographic and feeding conditions.

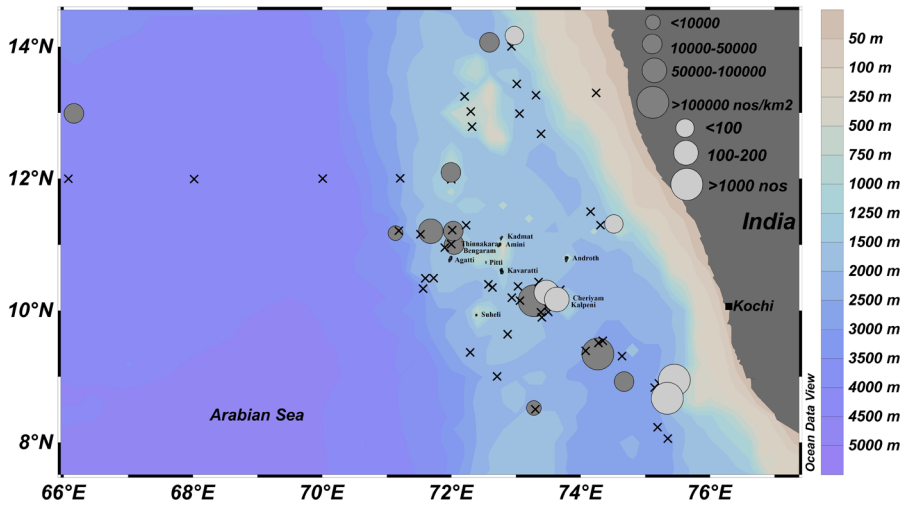

Fig. 11. – Map showing the abundance and distribution of paralarvae (cream white) and juveniles (grey) in southeastern Arabian Sea (Paralarvae number/1000 m^3, juveniles number/km^2 and (×) sampling stations.).

Both fin length and width showed positive allometry throughout the size ranges studied. Small fins of hatchlings provide little support for movement, but may counteract the tilting effect of the funnel jet (Staaf 2010). According to previous work on the closely related squid *Dosidicus gigas*, paralarvae ascend during mantle contraction and descend during mantle refilling; swimming is dominated by jet and sink swimming, where the fins are mainly used to stabilize (Staaf *et al*. 2008). Jet propulsion efficiency of juvenile and adults is significantly lower than that of paralarvae (Bartol *et al*. 2008). Juveniles and adults have more developed fins and use a combination of fin undulations and jetting, which can direct thrusts at any angle through a hemisphere below the body plane (Zuev 1964). Age and growth studies of paralarvae and juveniles revealed that the paralarval phase of *S. oualaniensis* in the Arabian Sea is about two months. They had a slow growth rate during the paralarval and early juvenile stages. The check mark in the statolith in early juvenile stage between 50 to 60 increments may indicate the end of the paralarval phase. Such check marks were also found in *D. gigas* (Chen *et al*. 2013), *I. argentinus* (Arkhipkin & Perez 1998) and *S. pteropus* (Lapitikhovsky *et al*. 1993). The formation of such check marks may also indicate delayed growth due to starvation from the splitting of the proboscis into two tentacles (Arkhipkin & Perez 1998).

Paralarval numbers were highest at the edge of the continental shelf and near the archipelago (Lakshadweep Island). A similar pattern has been reported in the Atlantic and Pacific ommastrephids *Illex illecebrosus, Todarodes pacificus* and *Ommastrephes bartramii* (Bower *et al*. 1999b, Young & Hirota 1990, O'Dor 1992, Dawe 1998) which have a life cycle similar to *S. oualaniensis*. Bower *et al*. (1999a) found evidence suggesting preferential spawning by *S. oualaniensis* near the Hawaiian Islands. High abundance of stage 1 paralarvae was observed in bottom depths of 425-931 m suggesting that most hatching occurred near continental shelf edge and slope. Enhanced prey availability may be one reason for spawning around the Lakshadweep archipelago. Entrainment of coastal water through convergent flows and confined upwelling cause phytoplankton and zooplankton to gather near the continental shelf area (Prakash & Ramesh 2007). Upwelling phenomena are reported to be one of the main regulators of the availability of food to early life stages of cephalopods and their growth, survival and recruitment (Vidal *et al*. 2010). Therefore, this plankton-rich zone may provide good feeding grounds for the presumably voracious paralarvae. In captivity, unfed *S. oualaniensis* paralarvae die six days after hatching (Sakurai *et al*. 1995). Okutani & Tung (1978) reported that juveniles of the species are frequently found aggregated in inshore waters around oceanic islands.

High abundance of paralarvae and juveniles were observed in January and February indicating that the peak spawning period was in December, and the presence of paralarvae and juveniles in March, April, October and November demonstrated that this species spawns throughout the pre-monsoon. Previously, Silas (1968) observed paralarvae of *S. oualaniensis* throughout the year except June and August from the west coast of India and Lakshadweep Islands.

The distribution of cephalopod paralarvae tends to be associated with distinct oceanographic features (Rodhouse *et al*. 1992, Ropke *et al*. 1993, Gonzalez *et al*. 2005), and environmental conditions have a major influence on both growth and recruitment success (Waluda *et al*. 2001). The distribution of the paralarvae of the complex *S. oualaniensis-D. gigas* (Cephalopoda: Ommastrephidae) were analyzed at the northern limit of the Eastern Tropical Pacific (Staaf *et al*. 2013, Sánchez-Velasco *et al*. 2016, Ruvalcaba-Aroche *et al*. 2018). Ruvalcaba-Aroche *et al*. (2018) concluded that the paralarvae of ommastrephidae inhabits the surface waters masses preferentially in convergence zones generated by mesoscale activity. Further, Sánchez-Velasco *et al*. (2016) state that the expansion of the depth range of hypoxic water may be increasing environmental stress on the paralarvae by vertically restricting their habitat, and so affecting their survival. Medium sized juveniles of *S. oualaniensis* were abundant in comparatively low zooplankton areas indicating changing feeding preference of juveniles (Mohamed *et al*. 2018). We also observed stomach contents of medium sized juveniles to display semi-digested fish bones, fins and squid eye lenses clearly indicating cannibalism. *Sthenoteuthis oualaniensis* may move inshore in pursuit of food but they are primarily denizens of the outer shelf and continental slope (O'Dor 1983). Chesalin & Zuyev (2002) report that the spawning of oceanic squids occurs in the open Arabian Sea, particularly the northern region of the Arabian Sea, but were not able to collect any eggs or egg masses. Earlier, under experimental conditions, eggs of the giant form of *S. oualaniensis* from Arabian Sea hatched out after 2.5 to 3 days at a temperature range of 21-25°C (Chesalin & Giragosov 1993). Our observations show that the earlier stages of paralarvae were distributed in continental shelf edge area and juveniles prefer more oceanic region, however, we were not able to collect any egg masses. Different size classes of paralarvae and juveniles show distinct spatial distribution patterns (Chesalin & Zuyev 2002). Juveniles were abundant both on the continental slope and high seas around Lakshadweep Archipelago. This indicates that juveniles prefer more oceanic regions and there is a distinct migration to the Arabian Sea basin from the continental slope.

This study is a first attempt to understand the paralarval and juvenile morphological development and migratory pattern of *S. oualaniensis* in the Arabian Sea. It demonstrated that paralarvae and earlier juveniles undergo different ontogenetic changes related to changes in habitat and lifestyle. The paralarvae were observed close to the continental shelf edge suggesting that spawning occurs

nearby, and the juveniles were abundant from the continental slope to the oceanic region suggesting they move to the oceanic region. Further detailed studies of the life history, particularly the influence of oceanographic variables are required for a complete understanding of these valuable unexploited stocks from the Arabian Sea.

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